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**MARINE TO ONSHORE VERTEBRATES IN THE
LOWER PERMIAN OF KANSAS AND THEIR
PALEOENVIRONMENTAL IMPLICATIONS¹**

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Abstract—Vertebrates occur together with marine-indicating invertebrates in the same facies of the Wreford Megacyclothem, Gearyan Stage, Lower Permian, of Kansas. The vertebrates include typically marine (petalodont, cladodont) taxa and those usually considered to be freshwater indicators (xenacanth, acanthodians). The consistent association of xenacanth and acanthodians with marine invertebrates and vertebrates in the Lower Permian of Kansas as well as their presence in both marine and freshwater lithofacies at other localities indicate that xenacanth and acanthodians were euryhaline, anadromous or catadromous, and so cannot be used as freshwater indicators. Burrows with the lungfish *Gnathorhiza* and the amphibians *Lysorophus* and *Diplocaulus* occur in nearshore green deposits, thus indicating that *Gnathorhiza* and late Paleozoic tetrapods of E. C. Olson's aquatic community were tolerant of salt water.

THE INVERTEBRATE FAUNA of parts of the Lower Permian of Kansas has been intensively studied with regard to its relationship to lithofacies and paleoenvironments. The Lower Permian Wreford Megacyclothem (Gearyan) has been particularly well investigated (Hattin, 1957; Cuffey, 1967; Lutz-Garihan and Cuffey, 1979). The environmental parameters show a change from fully marine to coastal (high-intertidal)

conditions. Vertebrates are common throughout the sequence, but all are fragmentary, with the exception of the lungfish *Gnathorhiza* and tetrapods at the base of the sequence (Speiser Shale); the latter occur in, or close to, burrows in close proximity to red deposits.

Lower Permian rocks in New Mexico, Texas, and Oklahoma yield an abundant and taxonomically diverse fauna of lower vertebrates (see Olson, 1958, 1977; Romer, 1958, 1960; Vaughn, 1966, 1969; Olson and Bolles,

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1975). These fossils occur in red deposits that are considered to be terrestrial or freshwater (Olson, 1977). In northern Oklahoma, these red deposits interdigitate with gray shales and limestones that contain marine invertebrate fossils (Lutz-Garihan and Cuffey, 1979). Red deposits, mostly shales, have a very limited distribution in the Lower Permian of Kansas (Hattin, 1957). Likewise, vertebrate fossils are much less common in the Permian of Kansas and have only occasionally been reported (Williston, 1897, 1899; Romer, 1925; Hotton, 1959; Williams, 1972; Coldiron, 1978; Schultze and Foreman, 1981).

Red deposits are considered to be the most terrestrial (nearshore to onshore) part of the Lower Permian cyclothems and megacyclothems of Kansas (Moore, 1966). Vertebrate remains are commonly used as terrestrial or freshwater indicators, even all the fish (T. H. Eaton in Lane, 1964). This traditional interpretation is mainly based on the fact that complete vertebrates most commonly occur alone, rather than together with invertebrates. In many cases, this isolation results from preservational biases (calcium phosphate versus calcium carbonate), and not paleoecological differences. Sometimes, the association of isolated elements of vertebrates with marine invertebrates has been explained as allochthonous, with the vertebrate remains having been washed in. No recent example of such association has been recorded. Here, I will present the relationship between the published invertebrate content and the vertebrate remains, extracted with acetic acid, from the same horizons throughout the Wreford Megacyclothem, Chase Group, Gearyan Stage, Lower Permian.

The Speiser Shale forms the base of the Wreford Megacyclothem. This formation has long been of interest to members of the Division of Vertebrate Paleontology of the Museum of Natural History, Lawrence, Kansas. The initial discovery of vertebrates at a Speiser Shale locality at Keats, west of Manhattan, Kansas, was made by J. M. Jewett in the 1930's. Hotton (1959) revived interest in the Speiser Shale and discovered a unique locality within the formation at Bushong, Lyon County, Kansas. The Bushong locality has a thick accumulation of isolated vertebrate bones of the kinds that occur in or close to burrows at other Speiser Shale localities. Orville Bonner and L.

D. Martin reopened the quarry at Keats in 1971. Subsequently, Orville Bonner and S. Dart in 1972, and R. W. Coldiron in 1974 continued to collect there (Coldiron, 1978). Brian Foreman was active from 1976 to 1980 at a new locality—Eskridge, Wabaunsee County, Kansas (Schultze and Foreman, 1981; Foreman, in press). The current project was started in 1979; R. R. West, Kansas State University, Manhattan, and Brian Foreman, Independence, Kansas, introduced me to the stratigraphy of the Wreford Megacyclothem. In 1980, Don Kirkpatrick discovered another locality with burrows containing vertebrate remains near Junction City in Geary County. The material is deposited in the vertebrate paleontology collection of the Museum of Natural History, University of Kansas (KUVP).

Acknowledgments.—Over the years, many people contributed to this project. I thank especially Brian Foreman, Don Kirkpatrick, and James McAllister for field work and preparations in the laboratory. Orville Bonner also helped in the field. R. J. Cuffey, Pennsylvania State University, supplied field notes and vertebrate fossils. SEM photographs were taken by Lorraine Hammer. I thank Mike Gottfried for improving the English. Janet Elder and Coletta Spencer typed the manuscript. The project was supported by grants 3275 and 3464 of the University of Kansas Graduate Research Fund, and by National Science Foundation grant EAR-8111721.

STRATIGRAPHY

The Wreford Megacyclothem (Hattin, 1957) includes two sedimentary sequences representing onshore to deeper marine deposits—the Threemile and Schroyer cyclothems. These comprise the top of the Council Grove Group (Speiser Shale) and the base of the Chase Group (Wreford Limestone and Wymore Shale Member of the Matfield Shale) within the Gearyan (Wolfcampian) Stage (Fig. 1). I follow assignment by the Geological Survey of Kansas (Zeller, 1968) of the Gearyan to the Lower Permian, which differs from practice of the Oklahoma Geological Survey (e.g., Simpson, 1973, 1979; Olson, 1975).

Three thick, cherty limestone units form the outstanding geomorphological feature in the north-south trending Flint Hills of central Kan-

chas. The thickest of the three, the Florence Limestone Member, lies above the Wreford Megacyclothem and is separated from it by the Blue Springs Shale and Kinney Limestone members. The Blue Springs Shale includes red deposits containing burrows with *Gnathorhiza* at least at one locality south of Manhattan, Kansas. The two other cherty limestone members, the Threemile and Schroyer, form the deepest

and most offshore part of the marine sequence. The Wreford Megacyclothem (for extensive descriptions, see Hattin, 1957; Cuffey, 1967; Lutz-Garihan and Cuffey, 1979) includes the sequence from the red middle Speiser Shale to the red middle Wymore Shale Member. This investigation extends the coverage to include the Funston Limestone below the lower Speiser Shale and the Kinney Limestone above the

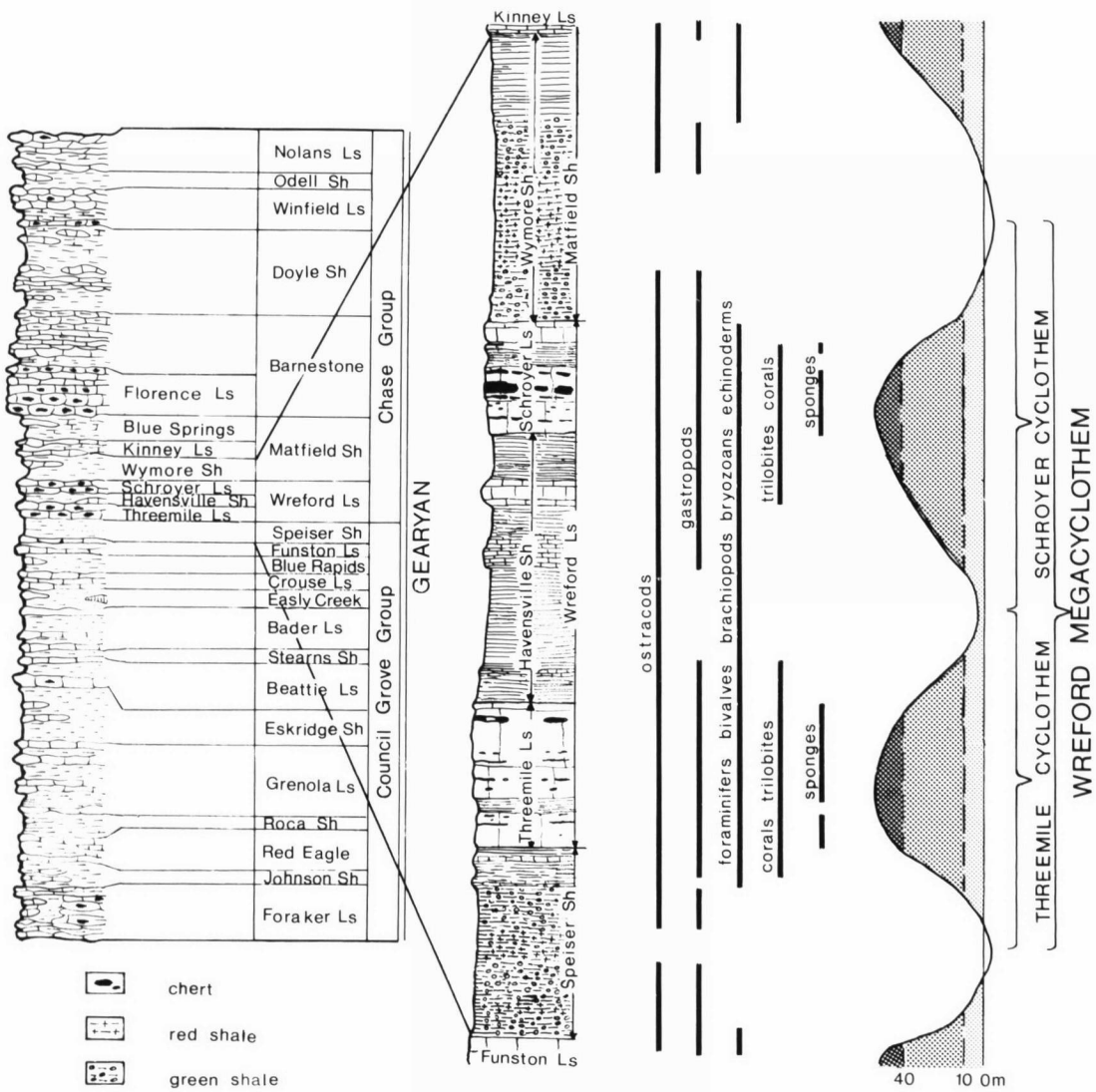


Fig. 1. Stratigraphic setting of the Wreford Megacyclothem, Gearyan, Lower Permian, in Kansas (after Zeller, 1968); distribution of invertebrates and interpretation of water depth after Hattin (1957).

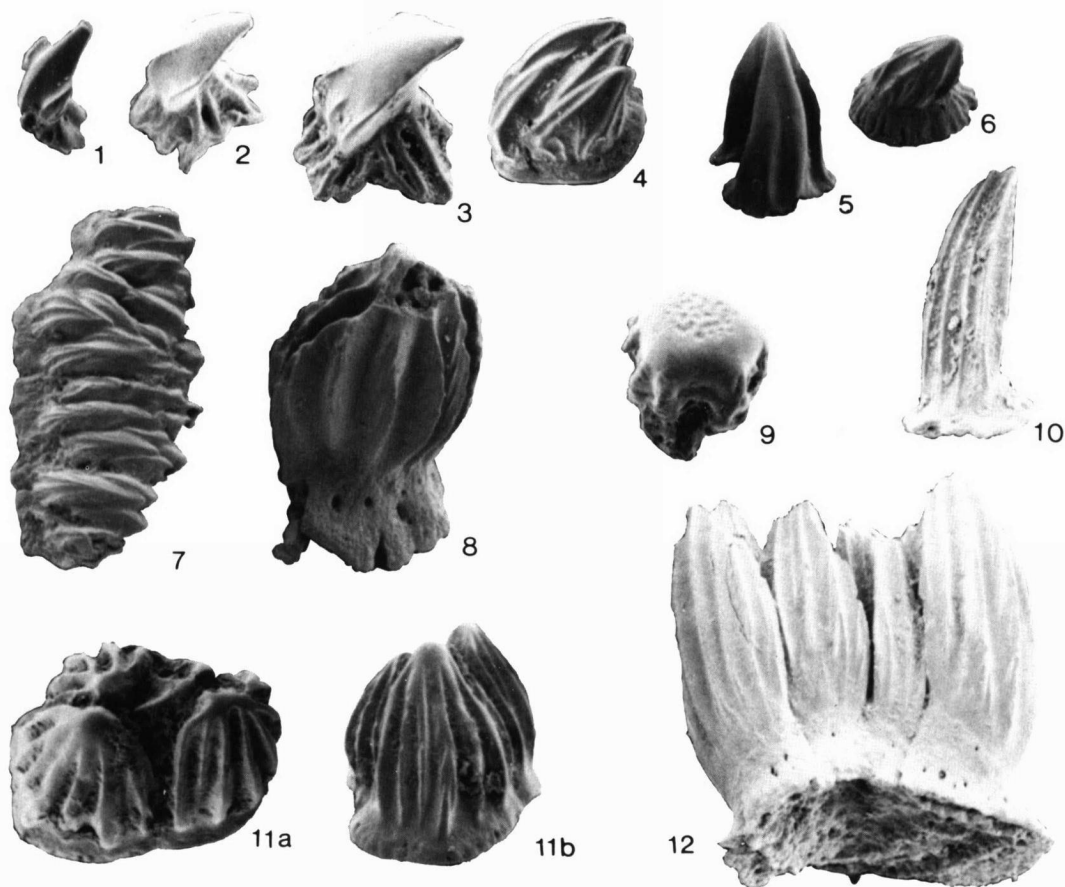


Fig. 2. Elasmobranchii indet., scales. —1-3. Simple placoid scales. 1, KUPV 82651, up. Havensville Sh., spillway just north of dam of Cowley Co. State Lake, SW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 8, T. 34 S., R. 6 E., Cowley Co., $\times 19$; 2, KUPV 82652, low. mid. Schroyer Ls., road cut on KS Hwy. 13, NE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 2, T. 16 S., R. 8 E., Morris Co., $\times 36$; 3, KUPV 82653, low. up. Havensville Sh., road cut, NE $\frac{1}{4}$ sec. 30, T. 29 S., R. 5 E., Kay Co., OK, $\times 38$. —4-8. Complex scales. 4, KUPV 82654, mid. Havensville Sh., road cut on Hwy. I-70, N $\frac{1}{2}$ SE $\frac{1}{4}$ sec. 29, T. 11 S., R. 9 E., Riley Co., $\times 19$; 5, 6, KUPV 82655, 82656, mid. Havensville Sh., road cut on Hwy. I-70, N $\frac{1}{2}$ SW $\frac{1}{4}$ sec. 27, T. 11 S., R. 8 E., Geary Co., $\times 20$; 7, KUPV 82657, low. Havensville Sh., road cut on KS Hwy. 38, SW $\frac{1}{4}$ sec. 19, T. 32 S., R. 8 E., Cowley Co., $\times 19$; 8, KUPV 82658, low. Schroyer Ls., road cut, NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 17, T. 25 S., R. 8 E., Butler Co., $\times 38$. —9. *Janassa* sp., KUPV 82659, low. Schroyer Ls., locality as for 1, $\times 19$. —10. Elongate scale, KUPV 82660, up. Havensville Sh., locality as for 1, $\times 20$. —11, 12. High complex scales. 11, KUPV 82661, up. Schroyer Ls., road cut on Hwy. I-70, NE $\frac{1}{4}$ sec. 34, T. 11 S., R. 6 E., Geary Co., 11a, dorsal view, $\times 20$, 11b, lateral view, $\times 20$; 12, KUPV 82662, low. Schroyer Ls., locality as for 1, $\times 20$.

upper Wymore Shale Member.

Lithology of the Wreford Megacyclothem has been well described (Hattin, 1957; Cuffey, 1967; Lutz-Garihan and Cuffey, 1979), and only a brief account is presented here. The light-gray, thick-bedded Funston Limestone is overlain by green shales of the lower Speiser Shale and red deposits of the middle Speiser. The upper Speiser can be subdivided into three

or four units of green, gray, and grayish-yellow, calcareous shale to limestone. The Threemile Limestone Member contains chert throughout its lateral and vertical extent except for the thin calcareous shale of its middle part, which contains little or none. The grayish-yellow, calcareous Havensville Shale Member with thin limestones separates the Threemile and Schroyer cherty limestones. The chert is found

mainly in the lower part of the Schroyer, whereas the middle Schroyer is represented by calcareous shales and the upper by algal (osagite) limestone. The middle part of the Wymore Shale contains, as does the Speiser Shale, red shales over- and underlain by green shales. The gray, noncherty Kinney Limestone is only 30 to 50 cm thick.

All units recognized by Cuffey (1967) within the sequence can easily be traced from Nebraska in the north to the Kansas-Oklahoma border in the south. The thicknesses change somewhat, the greatest being in central Kansas. The thickness of the sequence above the Speiser Shale decreases north- and southward; the thickness of the Speiser Shale increases southward. These minimal changes in thickness and lithology may indicate that the coast line of the Gearyan sea trended roughly north-south, with the distance from the shoreline changing little for each horizon throughout Kansas. This situation changes drastically in Oklahoma. The Speiser Shale (Garrison Shale) and Wymore Shale (Matfield Shale) increase in thickness of

constituent red shales and red channel sandstones, while the typical marine deposits of the Threemile Limestone, Havensville Shale, and Schroyer Limestone thin and disappear (Lutz-Garihan and Cuffey, 1979: pl. 1).

INVERTEBRATES AND PALEOENVIRONMENT

Rocks of the Wreford Megacyclothem contain a rich invertebrate fauna. Hattin (1957) listed the plant and vertebrate fossils for each lithofacies. Cuffey (1967) listed the distribution of bryozoan zoarial growth forms, Newton (1971) listed rhabdomesid bryozoans, Warner and Cuffey (1973) listed fistuliporacean bryozoans, Simonsen and Cuffey (1980) listed fenestrate, pinnate, and ctenostome bryozoans, and Lutz-Garihan (1976) listed various brachiopods, especially *Composita*.

The invertebrate groups are not evenly distributed throughout the sequence over all facies types (Fig. 1). Ostracodes and gastropods have the widest ranges. Ostracodes are absent

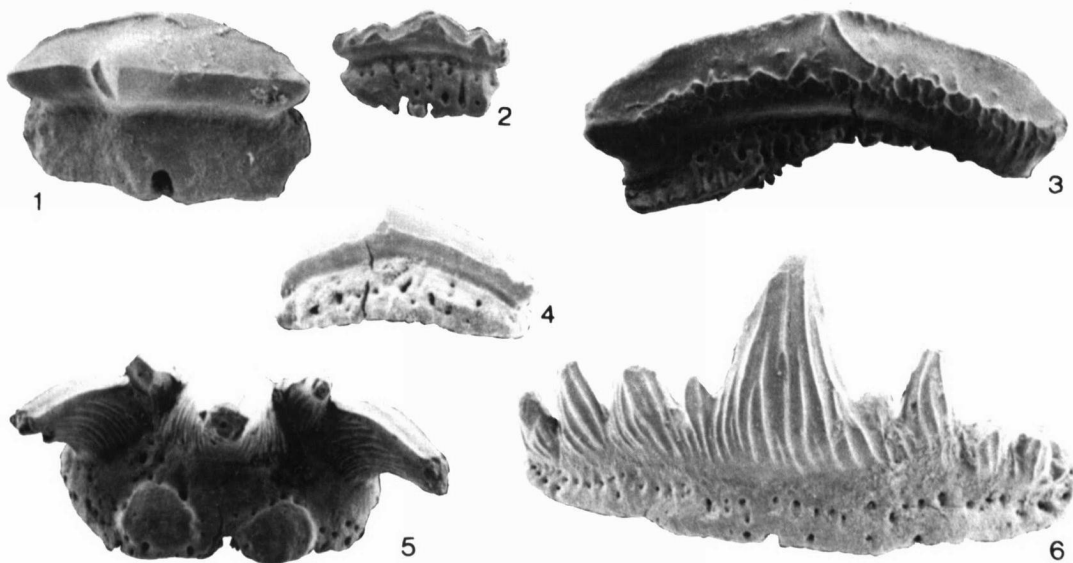


Fig. 3. Elasmobranchii, teeth. —1. *Elasmobranchii* indet., KUV 82663, low. Havensville Sh., road cut, SE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 16, T. 23 S., R. 9 E., Greenwood Co., $\times 36$. —2. *Desmiodus* sp., KUV 82664, low. Schroyer Ls., locality as for 1., $\times 19$. —3. *Hybodus* sp., KUV 82665, up. Schroyer Ls., road cut on Hwy. 1-70, N $\frac{1}{2}$ SE $\frac{1}{4}$ sec. 28, T. 11 S., R. 8 E., Geary Co., $\times 10$. —4. *Hybodus* sp., KUV 82666, mid. Havensville Sh., railroad cut, NW $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 31, T. 31 S., R. 7 E., Cowley Co., $\times 20$. —5. "*Cladodus*" sp., KUV 82667, up. Threemile Ls., road cut on KS Hwy. 13, SW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 28, T. 8 S., R. 8 E., Pottawatomie Co., $\times 19$. —6. "*Hybodus*" sp., KUV 82668, up. Threemile Ls., locality as for 4., $\times 20$.

only in red deposits; gastropods are absent in red deposits as well as in grayish-yellow mudstones (upper lower part of the upper Speiser Shale, middle Havensville Shale, upper Wymore Shale). Hattin (1957) found foraminifers, bivalves, brachiopods, bryozoans, and echinoderms only in deposits other than red and green shales. However, Cuffey (1967), Newton (1971), and Simonsen and Cuffey (1980) in detailed surveys of bryozoans, and Lutz-Garihan (1976) of brachiopods, found a wider occurrence of these two groups (see Fig. 9). Fenestellid bryozoans are present even in red shales, but Cuffey (1967), Newton (1971), and Simonsen and Cuffey (1980) favored an allochthonous interpretation for their presence—either by transport into the depositional environment or by redeposition from reworked older beds. The occurrence of brachiopods recorded by Hattin (1957) agrees with that of the marine species *Composita subtilita* (Lutz-Garihan, 1976), while *Derbyia* extends into green shale. Foraminifers, bivalves, and echinoderms are recorded by Hattin (1957) from the same horizons as brachiopods and bryozoans; there are, of course, natural local differences in abundance. According to Hattin (1957), corals and trilobites are restricted to calcareous shales and limestones, sponges to limestones.

Holocene occurrences of sediment types and invertebrates and the overlap between rock types and occurrence of invertebrates in the Wreford Limestone have been accepted as evidence supporting the thesis of cyclic changes of the depositional environment (Hattin, 1957; Moore, 1966). The red shales represent subaerial coastal-plain sediments on the most terrestrial end, and the cherty limestones represent the deepest or most offshore marine portion of the sequence. While Hattin (1957) accepted water depths up to 60 m, Cuffey (1967) and subsequent authors postulated fluctuations of lesser magnitude (water depth to 15 or 20 m; Simonsen and Cuffey, 1980). In conclusion, the paleoenvironment of the Wreford Megacyclothem is normal-marine, reaching brackish and subaerial conditions at its beginning and end.

VERTEBRATE DISTRIBUTION

Vertebrates occur as both isolated parts and

articulated specimens within the sequence. Isolated parts are common throughout the Wreford Megacyclothem, while articulated specimens occur only within, or close to, burrows in the green lower Speiser Shale. Above the sequence, small *Gnathorhiza* specimens occur in burrows of the red Blue Springs Shale (discovered by Brian Foreman in 1978); below the sequence, *Lysorophus* specimens were collected in 1974 by R. W. Coldiron in the upper green part of the Blue Rapids Shale.

In most cases, isolated parts of vertebrates are difficult to identify to genus or species. Tway (1979a) proposed an artificial numerical coding system for Paleozoic ichthyoliths based solely on the shape of elements. Consequently different parts of the same species appear under different code numbers. The cluster groups (Tway, 1979b: fig. 3) resulting from statistical analysis of these coded elements reflect neither taxonomic nor ecological groups. Representatives of different taxonomic units (as determined after Tway and Zidek, 1982, 1983) are included in the same cluster group (for example: palaeoniscoids, platysomoids, acanthodians, and different elasmobranchs in groups G_r and C_r). On the other hand, remains of the same group or genus appear in different cluster groups (for example, *Janassa* in groups F_r , E_r , etc.); this is to be expected if different parts of the same animal are classified only by shape. Tway's cluster groups may be the result of sorting by shape during deposition or an arbitrary consequence of the descriptor codes.

I prefer to use larger taxonomic units where specific identifications are not possible. Assignment to larger taxonomic units is easy and unambiguous. Chondrichthyans (Holocephali and Elasmobranchii), acanthodians, and actinopterygian osteichthyans are represented in the Wreford Megacyclothem, and can be often identified from ichthyoliths. No remains of iniopterygians, lungfishes, coelacanth, or rhipidistians have been identified, even though lungfishes are the most common vertebrates in the burrow fauna (lower Speiser Shale and Blue Springs Shale). The two occurrences of tetrapod remains (see Fig. 9) in the Wreford Megacyclothem may be explained as erratic—perhaps they were washed into the depositional environment.

Chondrichthyans are represented by different types of scales, identifiable teeth, and non-

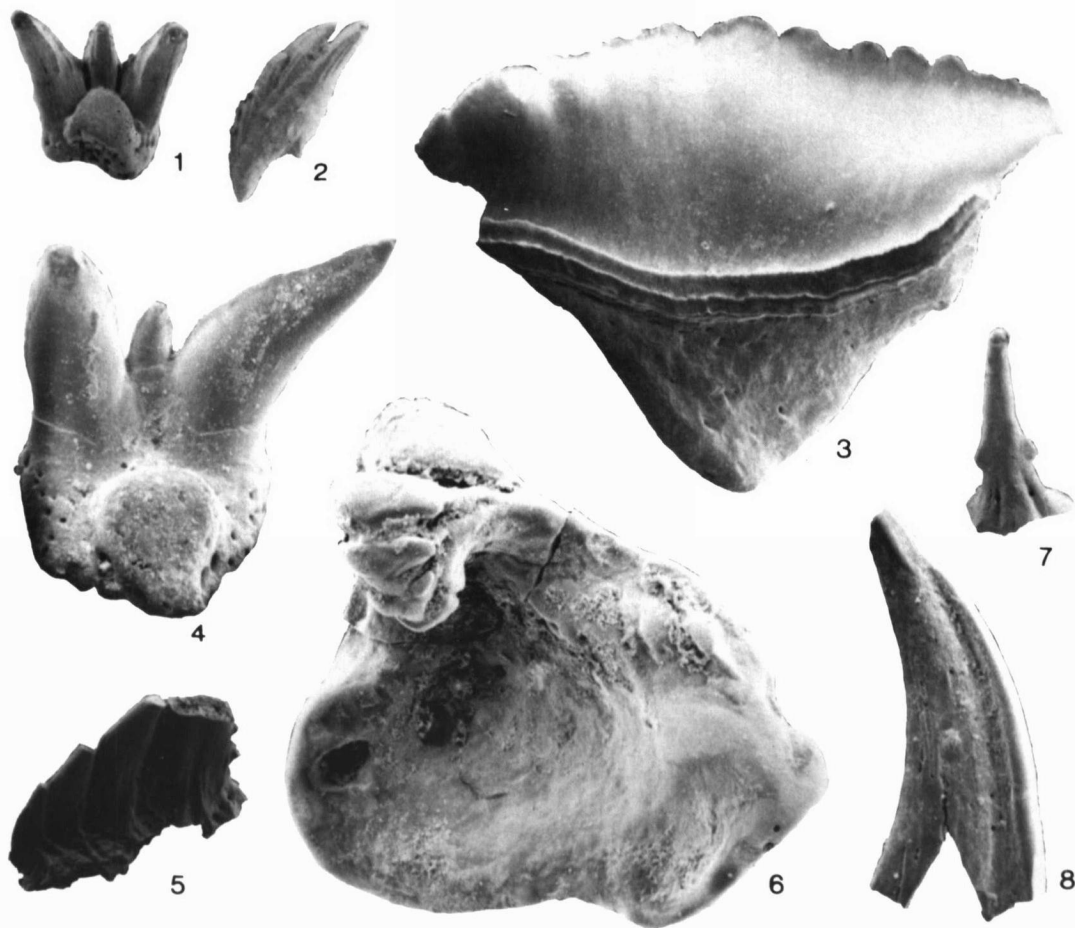


Fig. 4. Elasmobranch teeth (1-7) and acanthodian spine (8). —1. *Xenacanthus luedersensis*, tooth, KUPV 82669, Funston Ls., road cut on Hwy. I-70, NE $\frac{1}{4}$ sec. 34, T. 11 S., R. 6 E., Geary Co., $\times 18$. —2. "*Stemmatias*," mucous membrane denticle, KUPV 82670, low. Threemile Ls., road cut on US Hwy. 36, SE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 25, T. 2 S., R. 8 E., Marshall Co., $\times 19$. —3. Cf. *Serratodus*, tooth, KUPV 82671, mid. Havensville Sh., road cut on KS Hwy. 13, NE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 2, T. 16 S., R. 8 E., Morris Co., $\times 10$. —4. *Orthacanthus* sp., tooth, KUPV 82672, Kinney Ls., road cut on Hwy. I-70, N $\frac{1}{2}$ SE $\frac{1}{4}$ sec. 28, T. 11 S., R. 8 E., Geary Co., $\times 19$. —5. Mucous membrane denticle, KUPV 82673, up. Schroyer Ls., road cut, NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 17, T. 24 S., R. 8 E., Butler Co., $\times 18$. —6. Fused teeth of one-tooth family, KUPV 82674, low. low. up. Speiser Sh., road cut on KS Hwy. 38, SE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 20, T. 32 S., R. 8 E., Cowley Co., $\times 20$. —7. Branchial denticle, KUPV 82675, up. Schroyer Ls., locality as for 1, $\times 19$. —8. *Acanthodes* sp., apex of fin spine, KUPV 82676, mid. Havensville Sh., locality as for 1, $\times 19$.

diagnostic pieces of prismatic cartilage. Prismatic cartilage is not common because it disintegrates easily and isolated prisms are difficult to recognize. Chondrichthyan remains are the most common vertebrate fossils in acetic acid residues of limestones and calcareous shales of the Wreford Megacyclothem; scales are the most common remains, as would be expected from their numbers on the bodies of elasmobranchs. Simple placoid scales (Fig.

2, 1-3) have not been recovered as frequently as complex scales of different shapes (Fig. 2, 4-8, 11, 12). Scale type varies on different areas of the same individual in recent elasmobranchs, and the same scale type may be present in different species. Therefore, scales have been used to give specific identifications only in a few cases, mostly for Devonian and a few Carboniferous forms (see Zangerl, 1981:103-104). Complex scales are often

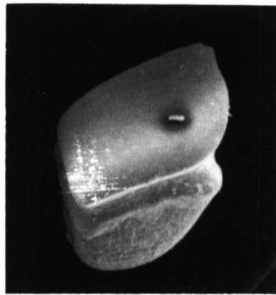


Fig. 5. *Acanthodes* sp., scale, KUVF 82677, mid. up. Threemile Ls., road cut on KS Hwy. 38, SW $\frac{1}{4}$ sec. 19, T. 32 S., R. 8 E., Cowley Co., $\times 40$.

formed by fusion of many scales (Fig. 2,11,12). The scales of *Janassa* (Ørvig, 1966; Malzahn, 1968) with their characteristic mushroom shape (Fig. 2,9) are very well known.

Elasmobranch teeth are often determined to species, even though the same type can occur in different genera ("*Cladodus*" is a typical example; see Zangerl, 1981:8,9,102). In addition, differently shaped teeth can occur in the same dentition (Zangerl, 1981:8). Still, a determination to genus and species is possible for some teeth, as with those of xenacanth. Hybodont (Fig. 3,3,4,6), cladodont (Fig. 3,5), petalodont (Fig. 4,3), and xenacanth (Fig. 4,1,4) teeth are common elements in the Wreford Megacyclothem, the diversity being higher than the few figures show. I am reluctant to identify some to genus or species (Fig. 3,1; 4,6), especially those that are mucous membrane denticles (Fig. 4,2,5,7). It is important for the paleoecological interpretation that xenacanth teeth and acanthodian scales occur together with a wide variety of elasmobranchs.

Acanthodians, which are not common in the sequence, are represented only by scales (Fig. 5). These are distinct from the scales of other fishes; nevertheless, their flat, smooth surface permits no specific identification. All scales may belong to *Acanthodes*, the genus represented in the Pennsylvanian and Permian of North America (Zangerl and Richardson, 1963; Simpson, 1973; Zidek, 1975a, 1975b, 1976, 1980). Acanthodians have been found from the middle upper Speiser Shale to the upper Schroyer Limestone, most commonly in the limestones, but also in the yellowish-gray shales of the middle Havensville Shale. In addition to scales, acanthodian fin spines (Fig. 4,8) have been found, but only at two localities (middle Havensville Shale in Geary County,

and middle upper Threemile Limestone in Cowley County).

Actinopterygians are represented by scales and teeth of palaeoniscoids and platysomoids. Actinopterygian teeth possess a characteristic acrodin tip (Ørvig, 1973, 1978) that is set off from the main part of the tooth (Fig. 6,3,4). The palaeoniscoid teeth are either conical with a widened base (Fig. 6,3) or roller-shaped with one pointed end (Fig. 6,4); some are preserved together on a piece of bone. Two toothed elements, presumably from the anterior upper jaw (Fig. 6,1,2), possess toothlike tuberculations on their outer side, similar to the rostral or antorbital bones of the Triassic *Redfieldius* (Schaeffer and McDonald, 1978: figs. 5, 6).

Palaeoniscoid scales show more variety than the teeth. The scale ornamentation ranges from smooth-surfaced (Fig. 7,1,3) to few elongate furrows on the surface and a serrated posterior border (Fig. 7,2,6,7), to separate ganoin ridges (Fig. 7,5) and elaborate ganoin ornamentation (Fig. 7,4,8,9). This variation indicates that there are at least four palaeoniscoid species present, but an identification to species is not possible at the present level of knowledge of palaeoniscoids and their scales. The different kinds of scales occur together in some samples. Sharp-ridged scales (Fig. 7,5) and serrated scales with furrows (Fig. 7,2,7) are represented in most samples, whereas smooth scales (Fig. 7,1,3) occur less commonly. Scales with elaborate ornamentation are very rare. Palaeoniscoid teeth and scales are not recorded from red (middle Speiser Shale, middle Wyomere Shale) and some green (lower and upper Speiser Shale) shales.

Centra (Fig. 8,1,2) occur together with palaeoniscoid teeth and scales at many localities. They belong to palaeoniscoids on the basis of their histology and occurrence with other palaeoniscoid elements (Schultze and Chorn, in press).

Platysomoids have the same distribution as palaeoniscoids. They can be recognized by their stout conical teeth (Fig. 6,5); sometimes sets of these teeth have been discovered occurring together on a bone ("phyllodont tooth plate," Johnson and Zidek, 1981; Fig. 6,6). It is more difficult to assign scales to platysomoids. Deep scales like those in Figure 7,10 show vertical ridges typical of platysomoids

(Bobasatraniaformes of Campbell and Le Duy Phuoc, 1983). Scales of platysomoids have been less frequently recognized (upper Funston Limestone in Riley County, Threemile Limestone in Cowley and Greenwood counties, lower Schroyer Limestone in Kay County, Oklahoma) than teeth. I tend to assign scales without ganoin but with bone sculpture (Fig. 7,11) to platysomoids. The assignment of the very rare scales with very elaborate sculpturing (Fig. 7,12) is uncertain; they may belong to platysomoids or palaeoniscoids.

Just below the red middle Speiser Shale, burrows occur in the upper part of the green lower Speiser Shale (see Fig. 10). Vertebrate fossils encountered in these burrows and their surroundings are often complete and represent forms that occur only rarely or not at all in other horizons (remains of dentitions and of vertebrae of indeterminate tetrapods in the lower Schroyer Limestone in Geary and Morris counties). The lungfish *Gnathorhiza* and the amphibians *Diplocaulus* and *Lysorophus* are found in the burrows, while the tri-

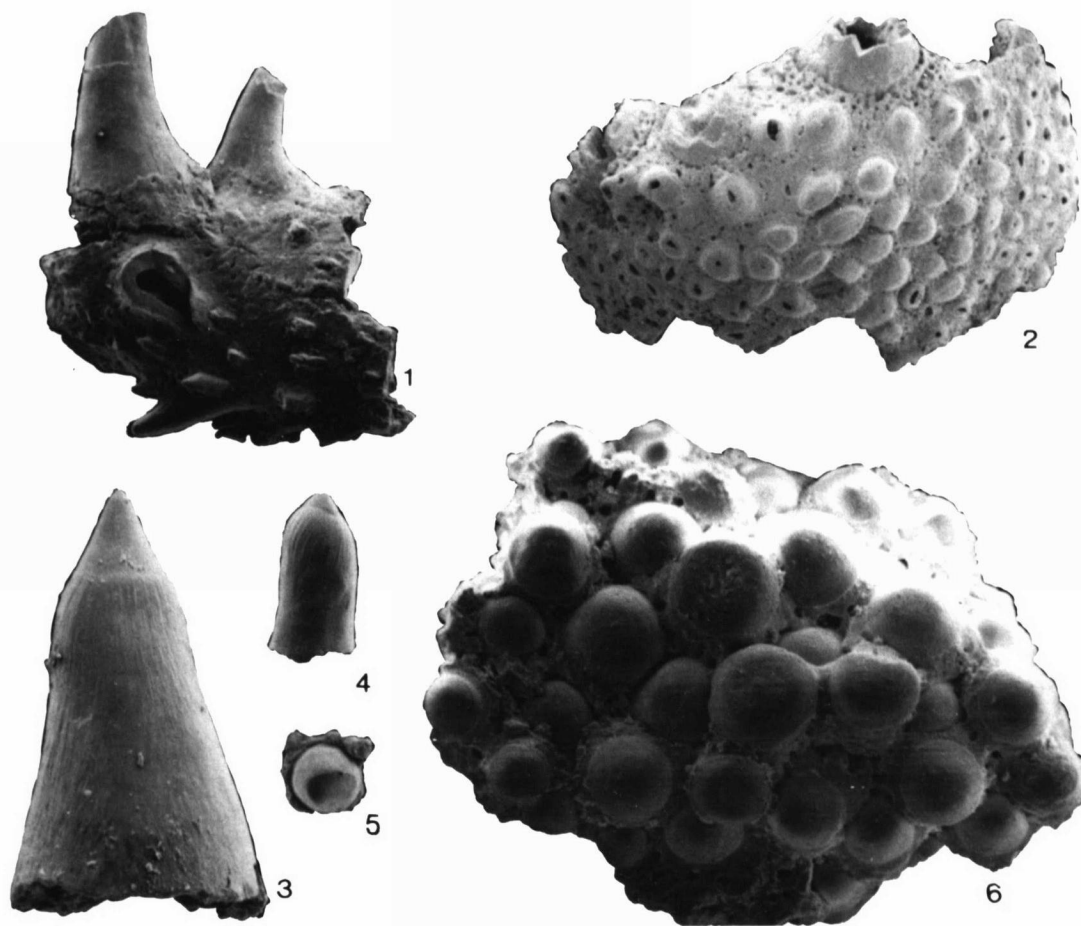


Fig. 6. Actinopterygian teeth.——1-4. Palaeoniscoid indet. 1, *Redfieldius*-like antorbital, KUPV 82678, low. Threemile Ls., road cut on KS Hwy. 13, SW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 28, T. 8 S., R. 8 E., Pottawatomie Co., $\times 19$; 2, premaxillar or antorbital, KUPV 82679, mid. up. Threemile Ls., road cut on KS Hwy. 38, SW $\frac{1}{4}$ sec. 19, T. 32 S., R. 8 E., Cowley Co., $\times 10$; 3, 4, isolated teeth, 3, KUPV 82680, up. Schroyer Ls., road cut on Hwy. I-70, NE $\frac{1}{4}$ sec. 34, T. 11 S., R. 6 E., Geary Co., $\times 38$, 4, KUPV 82681, mid. Threemile Ls., road cut on KS Hwy. 99, SW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 32, T. 13 S., R. 11 E., Wabaunsee Co., $\times 19$.——5, 6. Platysomoid indet. 5, single tooth with wear, KUPV 82682, up. Schroyer Ls., locality as for 3, $\times 19$; 6, convex phyllodont tooth plate, KUPV 82683, up. up. Speiser Sh., road cut, NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 17, T. 25 S., R. 8 E., Butler Co., $\times 20$.

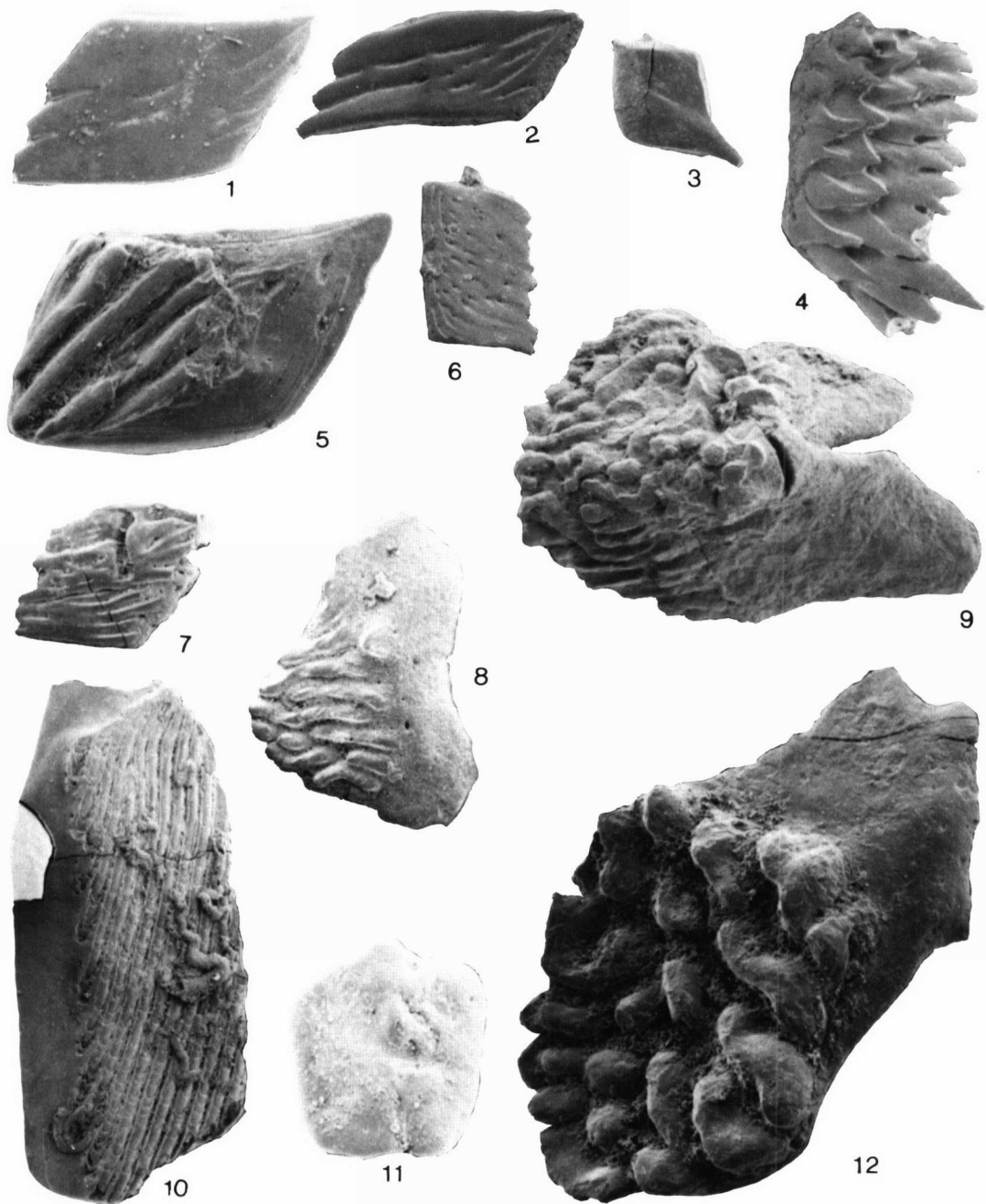


Fig. 7. Actinopterygian scales. — 1-9. Palaeoniscoid scales. 1, KUPV 82684, low. up. Havensville Sh., road cut, NE $\frac{1}{4}$ sec. 30, T. 29 N., R. 5 E., Kay Co., OK, $\times 20$; 2, KUPV 82685, low. Havensville Sh., road cut on KS Hwy. 38, SW $\frac{1}{4}$ sec. 19, T. 32 S., R. 8 E., Cowley Co., $\times 19$; 3, KUPV 82686, low. Schroyer Ls., road cut on KS Hwy. 13, SW $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 28, T. 8 S., R. 8 E., Pottawatomie Co., $\times 20$; 4, KUPV 82687, mid. up. Threemile Ls., road cut on US Hwy. 77, NE $\frac{1}{4}$ NE $\frac{1}{4}$ sec. 21, T. 4 S., R. 7 E., Marshall Co., $\times 20$; 5, KUPV 82688, low. low. up. Speiser Sh., road cut on KS Hwy. 38, SE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 20, T. 32 S., R. 7 E., Cowley Co., $\times 20$; 6, KUPV 82689, up. Schroyer Ls., road cut on Hwy. I-70, NE $\frac{1}{4}$ sec. 34, T. 11 S., R. 6 E., Geary Co., $\times 19$; 7, KUPV 82690, low. Schroyer Ls., road cut, SE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 16, T. 23 S., R. 9 E., Greenwood Co., $\times 19$; 8, KUPV 82691, low. Havensville Sh., road cut on KS Hwy. 13, NE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 2, T. 16 S., R. 8 E., Morris Co., $\times 19$; 9, median ridge scale, KUPV 82692, low. Threemile Ls., locality as for 3, $\times 20$. — 10-12. Platsomoid (10) or questionable platsomoid (11, 12) scales. 10, KUPV 82693, up. Funston Ls., road cut on Hwy. I-70, N $\frac{1}{2}$ SE $\frac{1}{4}$ sec. 29, T. 11 S., R. 9 E., Riley Co., $\times 19$; 11, KUPV 82694, low. low. up. Speiser Sh., locality as for 5, $\times 20$; 12, KUPV 82695, mid. Havensville Sh., railroad cut, NW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 31, T. 31 S., R. 7 E., Cowley Co., $\times 19$.

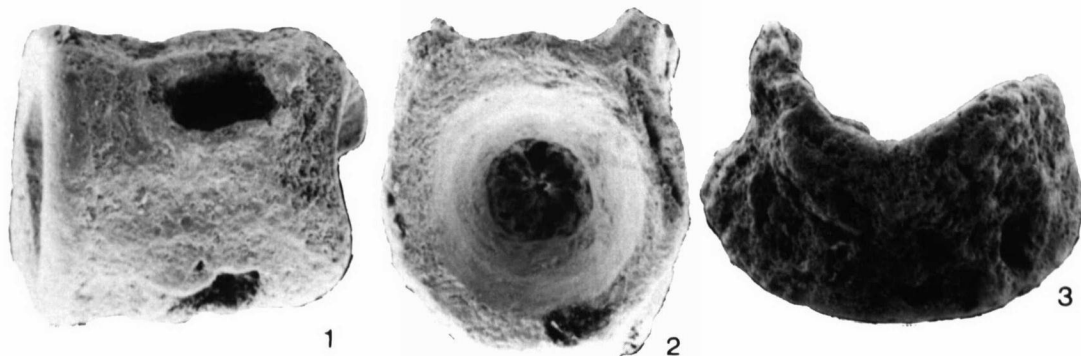


Fig. 8. Palaeoniscoid centra (1,2) and labyrinthodont ?intercentrum (3).——1-2. Palaeoniscoid centra. 1, From abdominal region in lateral view, KUPV 82696, low. low. up. Speiser Sh., road cut on KS Hwy. 38, SE $\frac{1}{4}$ SE $\frac{1}{4}$ sec. 20, T. 32 S., R. 7 S., Cowley Co., $\times 40$; 2, in anterior view, KUPV 81001, mid. up. Threemile Ls., road cut on KS Hwy. 99, SW $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 32, T. 13 S., R. 11 E., Wabaunsee Co., $\times 38$.——3. Labyrinthodont ?intercentrum in ventral view, KUPV 82697, low. low. up. Speiser Sh., locality as for 1, $\times 20$.

merorhachoid amphibian *Acroplous* and the microsauro *Euryodus* were not found inside burrows. All of these are aquatic vertebrates (Olson, 1977); only a few fragments of terrestrial reptiles and seymouriamorphs (from the "lake margin" of Olson, 1977) have been found. Palaeoniscoids, platysomoids, and elasmobranchs occur together with this fauna only in the bone coquina locality near Bushong, Lyon County.

VERTEBRATES AND PALEOENVIRONMENT

Cuffey's (1967) detailed analysis of the paleoenvironment of the Wreford Megacyclothem shows a marine depositional environment for central and southern Kansas, with red shaly intertidal deposition at the beginning and end of the sequence. The bryozoan *Fenestella* and the brachiopods *Composita* and *Derbyia* agree with the facies interpretation and are used here for comparison with occurrences of vertebrate remains (Fig. 9). The occurrence of *Fenestella* in the red middle Speiser Shale is interpreted as erratic (see above). Cuffey (1967) and Lutz-Garihan (1976) did not comment on bryozoans or brachiopods beyond the Wreford Megacyclothem, though they are found above and below the intertidal deposits at the beginning and end of that megacyclothem (see Fig. 1). All Wreford vertebrate remains are in marine rocks, except one elasmobranch fragment in the middle Speiser Shale discovered by R. J.

Cuffey in Greenwood County. The same explanation, that of erratic occurrence, used to account for the presence of *Fenestella* in the middle Speiser Shale is most plausible. Most vertebrates have a distribution similar to the bryozoan *Fenestella* or the marine brachiopods *Composita* and *Derbyia*; some were more restricted in deeper marine waters (e.g., cladodonts).

Palaeoniscoids, platysomoids, and elasmobranchs are distributed throughout nearly the whole marine sequence, missing only in the intertidal and some shallow water sediments (Fig. 9). Palaeoniscoids have been recorded from marine and freshwater sediments; as a group, they are not an indicator of either environment. Still, they are distributed here only within the marine part of the sequence, and some elements may be restricted to a marine environment. Thus, centra (Fig. 8, 1, 2) and *Redfieldius*-like toothed elements (Fig. 6, 1) occur together in the Lueders Formation (Lower Permian) of Texas as in the Wreford Megacyclothem of Kansas (Berman, 1970). The centra are known from the Lower Permian of southeastern Utah (Vaughn, 1967), different horizons in the Lower Permian of Texas (Berman, 1970; Johnson, 1979), the Lower Permian near Peru, Nebraska (Ossian, 1974) and the Upper Pennsylvanian near Topeka, Kansas (Schultze and Chorn, in press). While the Lower Permian of southeastern Utah was interpreted as marine, deposits at the other three

localities were considered to be marginal marine with terrestrial influx (Berman, 1970) or deltaic (Rasmussen and others, 1971; Ossian, 1974). They all contain marine invertebrates (bryozoans, brachiopods, echinoderms, ammonoids, bivalves) and vertebrates (different kinds of elasmobranchs and bradyodonts). Therefore, Schultze and Chorn (in press) concluded that palaeoniscoids with centra occurred in a marine environment.

Platysomoids are indicators of marine conditions; still, some Permian forms are reported from presumed freshwater deposits: *Schaefferichthys* (Dalquest, 1966), *Platysomus* (Simpson, 1974), and *Ebenaqua* (Campbell and Le Duy Phuoc, 1983). Therefore, habitat preferences of these fishes are uncertain (Johnson and Zidek, 1981) or varied. *Schaefferichthys* is one member of the rich fauna of the Lueders Formation (Wichita Stage, Lower Permian) of Texas (Berman, 1970; Johnson and Zidek, 1981; Johnson,

1981). The vertebrate composition of that fauna has great similarity to that of the Wreford Megacyclothem, but lacks the rich diversity of invertebrates. The same is the case with the *Platysomus* specimens in southern Oklahoma; plants are common, but invertebrates are lacking (Simpson, 1974). I prefer to interpret both faunas in light of the remains from the Wreford Megacyclothem (see below).

Ebenaqua is the most abundant species within an impoverished fauna of palaeoniscoids that occurs only in the Upper Permian of Australia between coal seams and together with plants (Campbell and Le Duy Phuoc, 1983). A freshwater environment is also postulated for some Carboniferous platysomoids (particularly *Chirodus*) in the Upper Carboniferous of Newsham, England, and of Linton, Ohio, which are placed in an open lake environment together with palaeoniscoids and petalodonts (Milner, 1980).

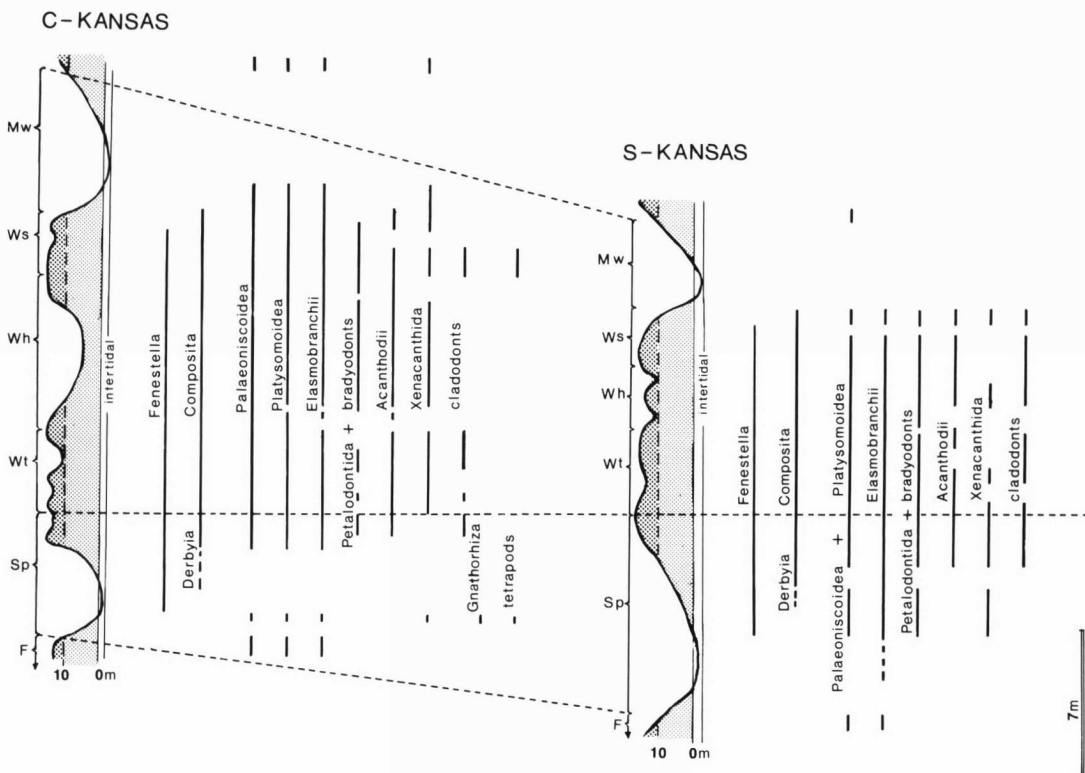


Fig. 9. Occurrence of vertebrate remains within the Wreford Megacyclothem compared with the occurrence of marine bryozoans and brachiopods in central Kansas (C: Riley, Geary, Wabaunsee, Morris, and Lyon counties) and southern Kansas (S: Chase, Greenwood, Butler, and Cowley counties); water depth after Cuffey (1967). F, Funston Ls. Fm.; Mw, Wymore Sh. Mbr.; Sp, Speiser Sh. Fm.; Wh, Havensville Sh. Mbr.; Ws, Schroyer Ls. Mbr.; Wt, Threemile Ls. Mbr.

Elasmobranch remains (scales, prismatic cartilage, and teeth) have a distribution nearly identical to that of palaeoniscoids and platysomoids (Fig. 9). Specific forms show a more limited extent within the sequence. Petalodonts (together with bradyodont remains, Fig. 9) are not recorded in all horizons in which elasmobranchs occur, but they show no consistent relationship to any specific marine environment. This is clearly not the case for cladodonts. The occurrence of cladodont teeth is restricted to sediments of deeper or more offshore marine environments, even though they are not always discovered in every one of these horizons. Xenacanth teeth show a distribution similar to that of cladodont teeth in the Wreford Megacyclothem of southern Kansas, but reach into shallower water deposits (especially in the central Kansas sequence).

The occurrence of petalodont and cladodont teeth within a marine sequence agrees with the published record (Zangerl, 1981). The association of xenacanth teeth with petalodont and cladodont teeth contradicts the interpretation of the former as indicators of freshwater (Zangerl, 1981). The taxa *Xenacanthus luedersensis*, *X. nebraskensis*, and *Orthacanthus* sp. have been recognized, these species occurring together with hybodont, cladodont, and petalodont teeth in the Lueders Formation (Lower Permian) of Texas, the Lower Permian near Peru, Nebraska, and the Upper Pennsylvanian near Topeka, Kansas. *Janassa* is another marine element common to all these localities. Xenacanth teeth (Tway and Zidek, 1983: fig. 45) are found together with cladodont teeth in marine deposits of the Upper Pennsylvanian (Shawnee and Lansing groups) of Kansas and in marine deposits of the Lower Carboniferous of England (Duffin and Ward, 1983:107). On the other hand, complete specimens of xenacanths are known from freshwater deposits in Europe (Fritsch, 1895; Boy, 1972) and from the red beds of Texas (Hotton, 1952), where they occur together with a diverse tetrapod fauna. It has to be assumed that xenacanths were tolerant of both salt- and freshwater; they could have been anadromous or catadromous.

Acanthodian scales are always found in deep-water limestones or calcareous shales, but they occur in low numbers within the shallow-water deposits of some middle Havensville Shale localities. *Acanthodes*, the most common

Carboniferous and Permian acanthodian genus, is said to be a freshwater indicator even though Denison (1979:17) cited many marine occurrences of this genus, especially in North America. As with the xenacanths, *Acanthodes* must have been euryhaline, anadromous or catadromous.

Remains of elasmobranchs, acanthodians, and actinopterygians occur within the marine sequence of the Wreford Megacyclothem. That is also true of the burrow fauna, with the lungfish *Gnathorhiza* and associated tetrapods. Fossil lungfish burrows have been compared to those of the recent lungfish of the genus *Protopterus* and, therefore, have always been taken for indicators of freshwater and of dry, seasonal climates (Romer and Olson, 1954). The association of lungfish burrows with tetrapods has been used as support for the freshwater evidence. Thus, the occurrence of typical lungfish burrows (Fig. 10) in nearshore marine sediments is surprising. Burrows occur at many localities in the lower Speiser Shale of central Kansas (Fig. 11), but only three localities contain specimens. This means only that in these examples the animals could not escape the sedimentation. *Gnathorhiza* was the main inhabitant of the burrows at the locality east of Junction City, while *Lysorophus* prevailed at the locality west of Eskridge, Kansas. The only explanation I can advance is that the burrows were used as retreats during tidal changes. This assumes that *Gnathorhiza* and the tetrapods were



Fig. 10. *Gnathorhiza* burrows from the upper part of the lower Speiser Shale, four miles east of Junction City, Kansas (NE 1/4 sec. 34, T. 11 S., R. 6 E., on Hwy. I-70), $\times 0.6$.

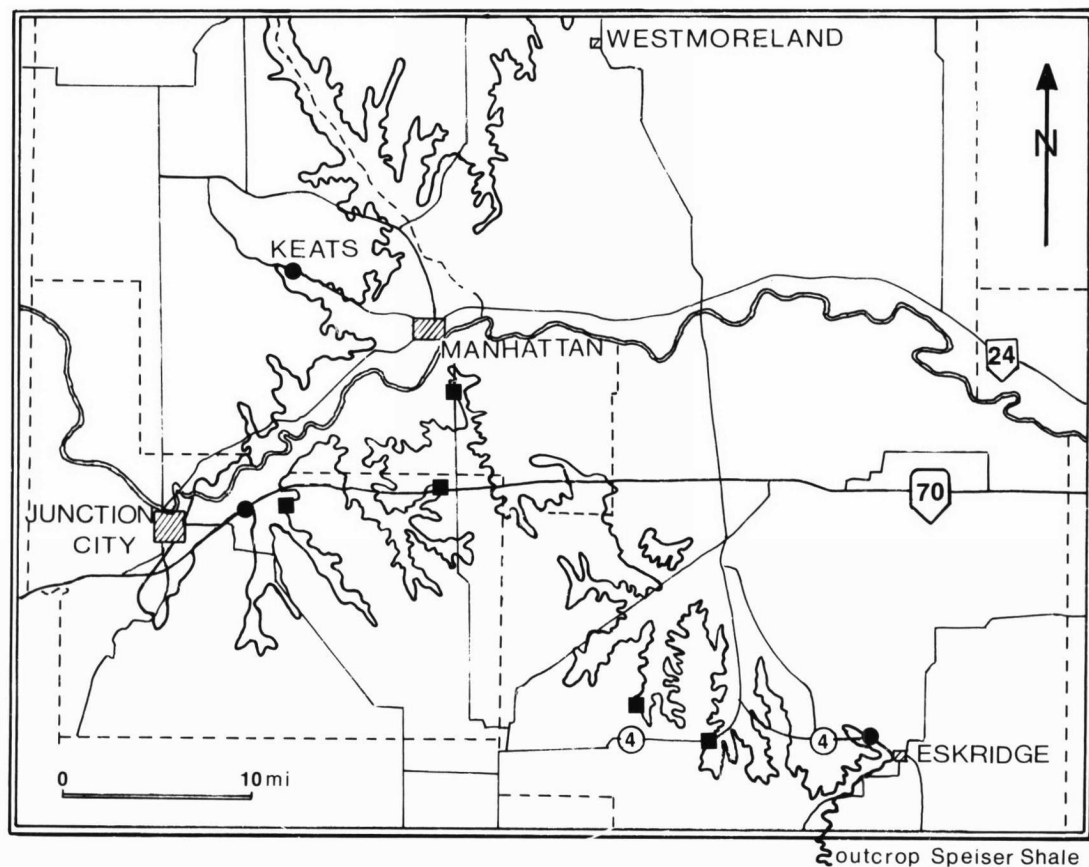


Fig. 11. Burrows in the Speiser Shale in central Kansas with (black circles) and without (black squares) vertebrate fossils.

tolerant of salt water. *Gnathorhiza* remains occur in stromatolites in the Upper Pennsylvanian of northeastern Kansas together with marine invertebrates, petalodonts, hybodonts, and cladodonts—an assemblage very similar to that in the Wreford Megacyclothem. Extant amphibians are intolerant of salt water, with very few exceptions (for citations, see Schmidt, 1957) such as *Rana cancrivora* (Gordon and others, 1961) and some *Rana sphenoccephala* (Christman, 1974). Extant amphibians are far removed from the Paleozoic ones, and it may be that the fossil aquatic genera (Olson, 1977) are not lacustrine, but rather marine forms. Additional evidence for the occurrence of the burrow fauna within the marine environment can be deduced from the lower Speiser Shale locality near Bushong, Lyon County, Kansas. At that locality, bones of *Gnathorhiza* and the amphibians of the

burrow fauna are accumulated in a lens, a bone coquina, together with vertebrate remains of the marine sequence (Fig. 9). This has to be interpreted as the result of sweeping together (by storm?) of the burrow fauna from the seaside to the shore.

COMPARISONS

Statements of the environmental preference of a species are empirical, particularly for fossil forms. It is difficult to propose a testable hypothesis for paleoenvironmental preference. The time-span between Paleozoic and Holocene is so great that one cannot be certain that today's preference can be assumed for distantly related Paleozoic forms. Hence, I prefer to use the association of vertebrates with undoubted marine invertebrates as the most reliable indi-

cators of a marine paleoenvironment. There are no definitive freshwater indicators in the Paleozoic. Low diversity of the vertebrate fauna and the lack of marine invertebrates are often used as freshwater indications, but I am not sure how much one can trust assignments to freshwater based on those criteria. Nevertheless, I will accept these assignments here for the purpose of comparison.

The occurrence of *Acanthodes* and xenacanthids together with marine invertebrates and vertebrates has been recorded earlier, even though both forms are frequently cited as freshwater indicators. Xenacanthids and *Acanthodes* are cited from the freshwater Braidwood and the marine Essex faunas in the Upper Pennsylvanian of the Mazon Creek area, Illinois (Bardack, 1979), and from the freshwater Garrard locality and the marine Logan and Mecca localities in the Upper Pennsylvanian of Indiana (Zangerl and Richardson, 1963). In both cases, there is a significant difference in diversity of the marine and the freshwater environments, the former having far more forms. Palaeoniscoids and platysomoids occur in both environments in the Mazon Creek area (Bardack, 1979); the platysomoid *Chirodus* is known from another Late Pennsylvanian freshwater locality at Linton, Ohio. Lungfish occur in the marine Essex fauna (Schultze, 1975, 1977), while amphibians are known from the marine Essex and the freshwater Braidwood faunas of the Mazon Creek area. The amphibians in the marine Essex fauna are interpreted as erratics by Milner (1982).

A vertebrate fauna as rich as that of the Wreford Megacyclothem has been described from the Lower Permian at Peru, Nebraska (Ossian, 1974), and the Lower Permian of Texas (Berman, 1970; Johnson, 1979). The Peru locality contains a high diversity of invertebrates, with bryozoans, brachiopods, echinoderms, ammonoids, and bivalves, all indicating a marine environment, as do the marine clasmobranchs (*Deltodus*, *Campodus*, *Caseodus*, *Petalodus*, "*Cladodus*"). Acanthodian scales, xenacanth teeth (*Xenacanthus nebraskensis*, *Orthacanthus* sp.), lungfishes (*Gnathorhiza*, *Sagenodus*), and amphibians (*Diplocaulus* and others) are represented in the same fauna, as are *Redfieldius*-like antorbital. Ossian (1974) interpreted the depositional environment as that of a deltaic sequence comparable to the Rhône delta

in France. Marine fishes travel far up the Rhône delta and replace the freshwater fauna. That explains why deltaic deposits can contain marine but not freshwater fishes.

The localities in the Lueders Formation, Lower Permian of north-central Texas, furnished a very diverse vertebrate fauna (Berman, 1970; Johnson, 1979) similar to that in the Wreford Megacyclothem but having coelacanth, more terrestrially adapted amphibians (*Eryops*, *Diadectes*), and reptiles. Palaeoniscoid centra and *Redfieldius*-like antorbitals also occur there. The combination of marine chondrichthyans with xenacanth, acanthodians, *Gnathorhiza*, and tetrapods is interpreted as a mixed fauna in a nearshore or estuarine environment (Johnson, 1981) where the "freshwater and terrestrial" elements were washed in.

The burrow faunas in the Lower Permian of Texas and Oklahoma have always been regarded as freshwater indicators (Olson and Bolles, 1975), by comparison with recent freshwater burrows. In these faunas, *Gnathorhiza* occurs with amphibians that Olson (1977) considered part of the aquatic community. These amphibians are found together with marine vertebrates and invertebrates in the Upper Pennsylvanian of northeastern Kansas (Chorn and Conley, 1978) and in a burrow fauna in the lower Speiser Shale of central Kansas.

CONCLUSIONS

The comparison of vertebrates from the Wreford Megacyclothem with those from other Upper Pennsylvanian and Lower Permian localities in North America demonstrates that:

- 1) There are no freshwater-indicating vertebrates known at present. The supposedly freshwater-indicating xenacanth, acanthodians, and lungfishes occur in both marine and freshwater paleoenvironments.

- 2) Recent lungfish burrows, with their restriction to freshwater environments, are not comparable to those of lungfish of the Late Paleozoic. Fossil burrows occur in marine, nearshore deposits, and the lungfish *Gnathorhiza* itself in such marine deposits as Upper Pennsylvanian stromatolites in northeastern Kansas (Chorn and Conley, 1978).

- 3) The association of *Lysorophus*, *Acroplous*, and *Diplocaulus* in the burrow fauna with *Gnathorhiza* implies that these forms were salt-

water tolerant. Elements of this aquatic community of Olson (1977) occur together with marine forms at many localities, but they have previously been explained as erratic, from freshwater or terrestrial habitats. As an excep-

tion, Parrish (1978) postulated a tolerance for brackish to marine conditions for *Xenacanthus*, *Trimerorhachis*, *Diplocaulus*, *Eryops*, *Archeria*, *Ophiacodon*, and *Dimetrodon* based on paleogeographical evidence.

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